

Common Constructal Principles in Design of Transportation Networks in Plants and Animals

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Abstract

Common principles of design of long-distance liquid transport in the nature are discussed. Some results of measurements on the preparations and casts of the large systemic and small and medium intraorgan arteries are presented. The regularities between the diameters and the branching angles of the arteries in the bifurcations are revealed. The results of measurements on the conducting systems of plant leaves with different shape, size and type of the vasculature are also presented and compared to the arterial vasculatures. It is found the principles of construction are the same in the transportation networks of animals and higher plants and correspond to the model of optimal branching pipeline that provides liquid delivery at minimal total energy costs. A relationship between the length of the path along any subtree of the pipeline and the corresponding drainage area has been found for the leaf venation. The relationship corresponds to the Hack's law revealed for the river basins. A model of the steady flow in the pipeline with permeable walls is proposed for the liquid delivery in the leaves. It was found, a balance between the inflow of the liquid into a subtree and its consumption by the cells in the corresponding area leads to the Hack's law. A comparative study of the hydraulic conductivity of the leaves of different evolutionary age is carried out and validity of the constructal law is shown.

1. Introduction

Special transportation systems for the long-distance delivery and distribution of biofluids are common for the multicellular organisms. The liquid (gas) with some dissolved components (oxygen, carbonic acid, mineral and organic nutrients) must be delivered to a distributed set of consumers (cells, tissues, organs). In the nature the fluid transportation problem is solved by constructing branching networks formed by ducts or tubes with a gradually decreased caliber. Such pipelines can be found in mammals (arterial and venous systems (Fig1.a), bronchial tree, and nervous networks), plants (xylem and phloem conducting systems in roots, shoots, stems, and leaves (Fig.1b)), invertebrates and some other animals and river basins (Fig.1c). In spite of the complicated topology of the networks the experimental investigations revealed some common design principles of construction of the conducting systems in the nature [5,6,14,20,24]. The principles express certain relationships between the lengths L_j and diameters d_j of the consecutive vessels and branching angles α_j in the bifurcations of the conducting elements (Fig.1d).

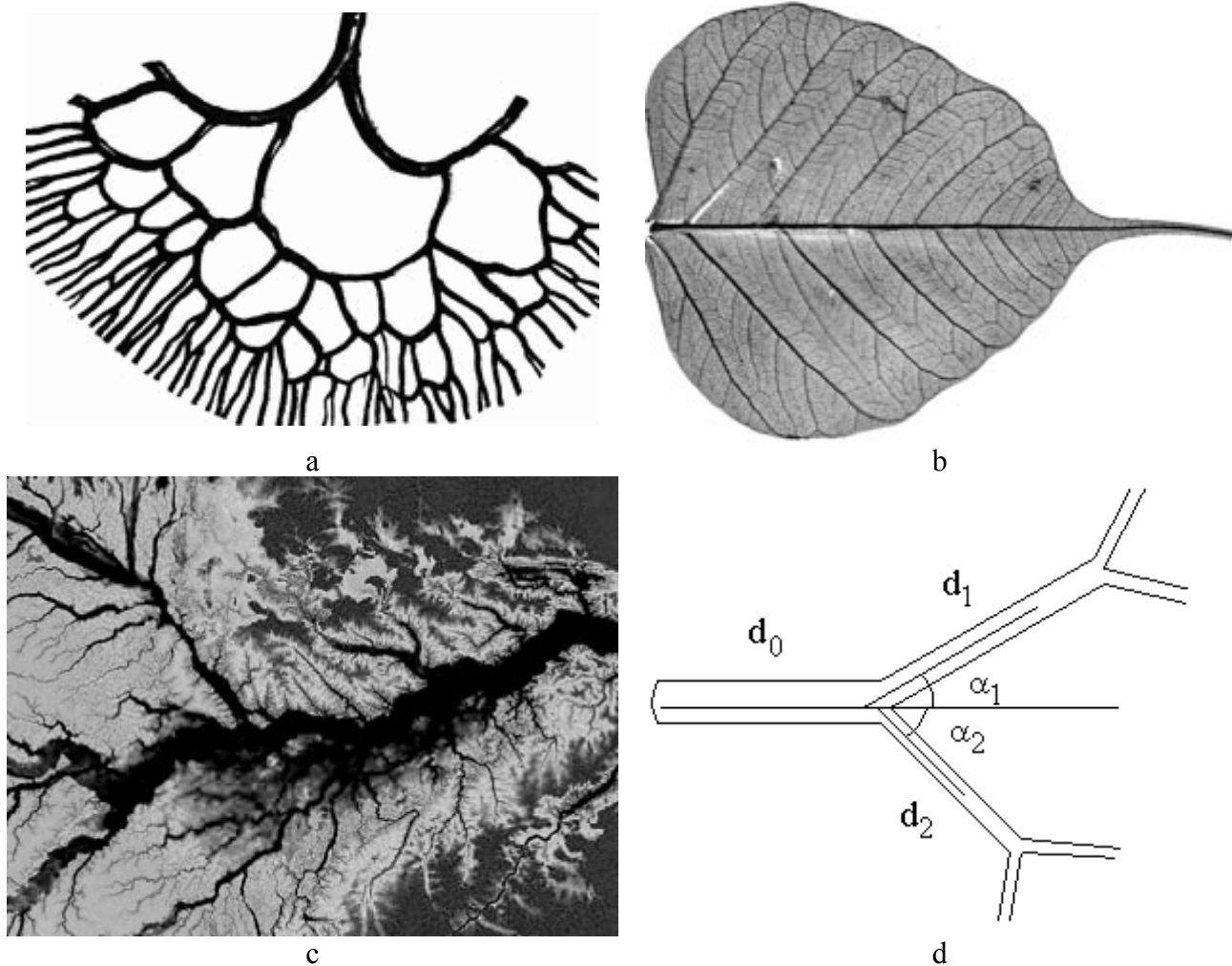


Figure 1 - Schematics of the arterial system of the small intestine (a), a leaf (a), Amazon basin (c) and a single bifurcation of the conducting elements (d)

2. Experimental data on the optimal properties of the fluid transport networks in Nature.

2.1. Relationships between the diameters of the tubes in a bifurcation.

During the vast measurements on the plastic casts and preparations of mammalian arterial [1,14,20,25], venous [14,20] and respiratory [14,25] systems, trophic fluid transport systems in sponge [1], tree trunks and shoots [8-9], and plant leaves of different types [5,6,7-9] the statistical dependence

$$d_0^\gamma = d_1^\gamma + d_2^\gamma \quad (1)$$

have been obtained. Here d_0, d_1, d_2 are the diameters of the parent and daughter's vessels at a bifurcation, and the power exponent γ was found to be $\gamma = 2.55 - 3.02$ for arterial systems, $\gamma = 2.76 - 3.02$ for venous systems, $\gamma = 2.61 - 2.91$ for respiratory systems. On an average $\gamma \approx 3$ and the higher the animal's position at the evolutionary scale, the closer γ to 3 [25]. For the blood large vessels where flow is not laminar (aorta, respiratory trunk) $\gamma \approx 2.33$ has been obtained [22]. In the small vessels the blood exhibits non-Newtonian properties and $\gamma \approx 2.92$ in (1).

The own detailed measurements on the preparations and plastic casts and ultrasound measurements on the alive patients revealed some differences in the relationship (1) [10,11,26]. The inner organs have been obtained by autopsy from cadavers when death of young healthy subject had been caused by asphyxia. The casting polymer which is initially a liquid, was injected through the feeding arteries at a physiological pressure $P=80$ mm Hg. After polymerization of the polymer the organs

have been kept into the sulphuric acid during 72 hours and rinsed with water then. As a result the accurate 3d-replicas of the networks have been obtained. The successive nodes of each cast have been enumerated and the replicas have been broken into pieces for the purpose of measurements. The diameters of the separate elements of the replicas correspond to the inner diameters of the arteries of the vasculature. If one introduces an asymmetry coefficient $\xi = d_{\min} / d_{\max}$, where $d_{\min} = \min\{d_1, d_2\}$, $d_{\max} = \max\{d_1, d_2\}$, (1) can be rewritten as $d_{\min} = \xi d_0 \Xi$, $d_{\max} = d_0 \Xi$, where $\Xi = (1 + \xi^\gamma)^{-1/\gamma}$. In that way one can expect the relationships $d_{\min}(d_0)$ and $d_{\max}(d_0)$ predicted by (1). Some measurement results are presented in Fig.2. The measurements on the coronary tree have been carried out on 5 human plastic casts with accuracy 0.1mm. The parameters of the bifurcations of systemic arteries have been measured in the course of the post-mortem examination of 5 corpses (database I). Each artery has been followed down to the place at which it penetrates into an inner organ or a muscle. The diameters and lengths of the systemic arteries and feeding arteries of the inner organs have also been measured in 5 healthy volunteers (with age ranging from 18 to 42) using triplex scanner ‘Sonolaine Elegra Advanced’ Siemens (database II). The calculated dependences $d_{\min}(d_0)$ and $d_{\max}(d_0)$ are compared in Fig.2c-d to the measurement data obtained on corpses in the very first 55-tube model of the systemic arterial tree [23]. The measured diameters of the arterial segments in both replicas and corpses correspond to the inner diameters of the arteries at the maximal dilatation.

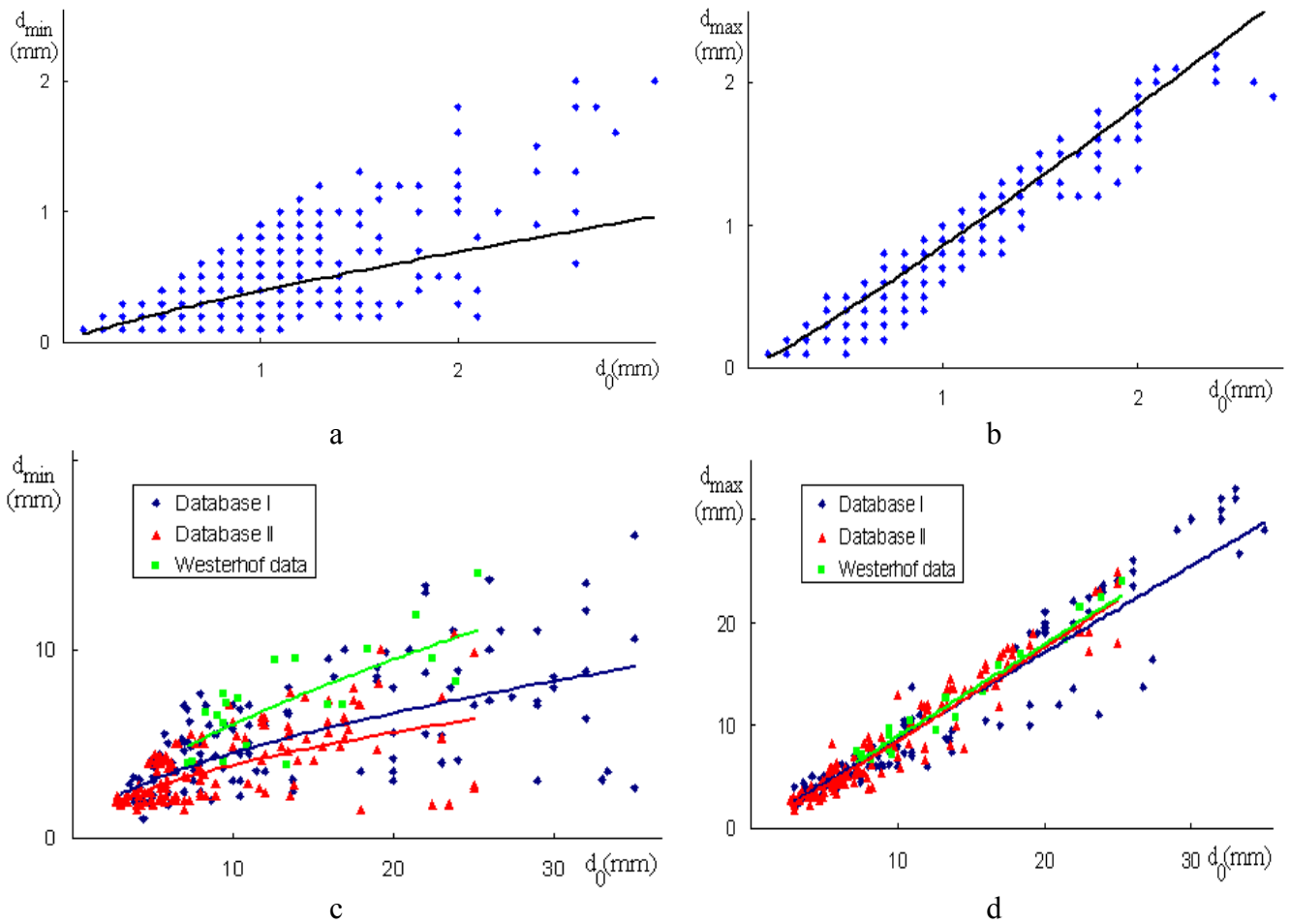


Figure 2 - Dependences $d_{\min}(d_0)$, $d_{\max}(d_0)$ for the coronary (a,b) and systemic (c,d) arterial trees

As one can see a strong linear dependence is proper to the statistical relationship $d_{\max}(d_0)$ for both systemic and intraorgan arterial junctions. The approximation $d_{\max} = \alpha d_0^\beta$ has been found

($\alpha = 0.883$; $\beta = 0.99$; $R^2 = 0.915$ for database I; $\alpha = 0.756$; $\beta = 1.05$; $R^2 = 0.902$ for database II and ($\alpha = 0.873$; $\beta = 1.01$; $R^2 = 0.933$ for the Westerhof data) (Fig.2d). In that way $d_{\max} \sim d_0$. The scatter in the dependence $d_{\min}(d_0)$ is bigger and some differences in least square approximations have been found for the studied vasculatures (Fig.2a,c).

Own measurements on the digital images of the leaves of 39 families with different size (0.5-40 mm), shape and venation type revealed similar dependencies between the diameters of the veins in the bifurcations. The perfect linear dependences $d_{\max}(d_0)$ and quite good linear approximations $d_{\min}(d_0)$ have also been discovered for all the investigated leaves. For the example plotted in Fig.3b the linear approximations are $d_{\max} = 0.952d_0 - 0.225$ ($R^2 = 0.977$) and $d_{\min} = 0.323d_0 + 2.353$ ($R^2 = 0.759$).

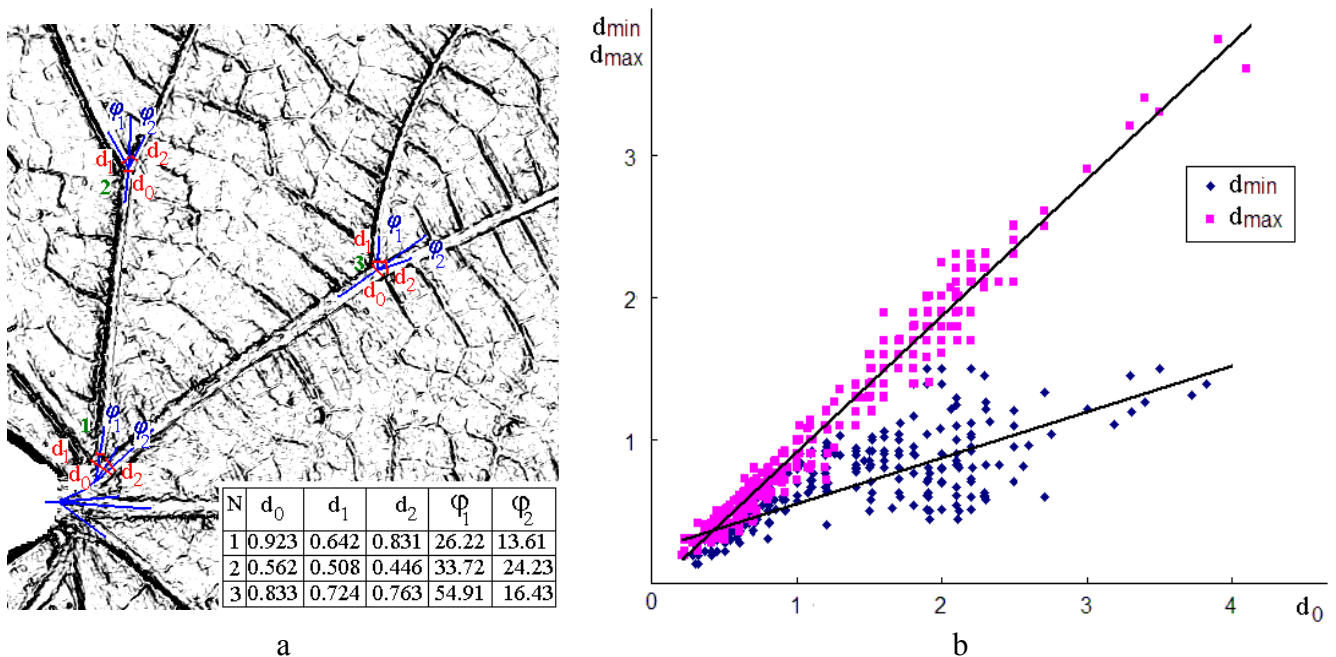


Figure 3 - Software for image analysis of the leaf venation (a) and the dependences $d_{\min}(d_0)$ and $d_{\max}(d_0)$ for a *Cotinus Obovatus* leaf blade (b). Solid lines correspond to the linear approximation of the statistical dependences

The statistical dependences $d_{\min,\max}(\xi, K, \mu)$, where K and μ are branching ratio and optimality coefficient are also the same for the vascular bifurcations and junctions of the plant leaf conducting elements.

2.2. Relationships between the branching angles and diameters of the conducting elements.

The results of own measurements for the dependences $\alpha(d_0)$, where $\alpha = \alpha_1 + \alpha_2$ for the arterial vascular beds and leaf venations are presented in Fig.4.

Similarities in the dependences $\alpha(\xi)$, $\alpha_{1,2}(d_{1,2})$ and $\alpha_{1,2}(\xi)$ are also similar for both mammalian vasculatures and the conducting systems of plant leaves. For the relatively large vessels (veins) the branching angle may be constant (fig.4b) or linearly decreasing function of the angle (fig.4a). For the small and medium vessels the scatter in the branching angle is observed within certain limits. The same sort of dependences has been obtained for the arterial bifurcations by different authors [15,16,21]. For the leaf venations the similarity between the animal and plant conducting systems has been revealed by the authors [5-9].

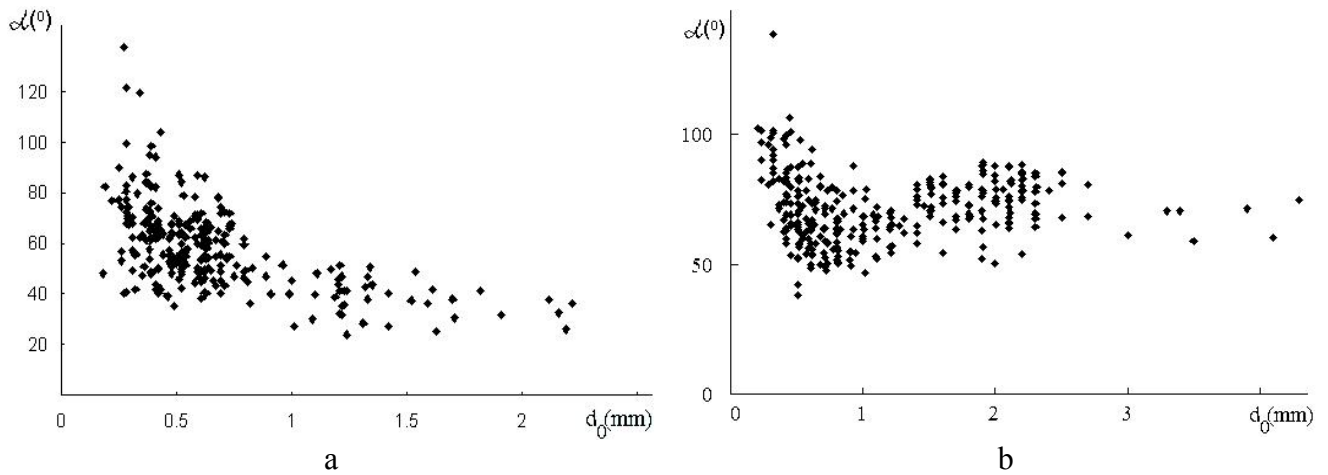


Figure 4 - Dependences $\alpha(d_0)$ for the brain arteries (a) and *Phaseolus vulgaris* leaf venations (b)

2.3. Relationships between the conducting pathways and drainage areas.

Detailed measurements on the satellite pictures of the river basins revealed a strong dependence between the length L_Σ of a tributary of the river system and its drainage area S_Σ , i.e. the area covered by the tributary with all its branches [2,4]. The dependence $L_\Sigma \sim S_\Sigma^\vartheta$, $\vartheta = 0.5 - 0.6$ has been obtained and is called the Hack's law. It can be substantiated by the balance between the water uptake over the drainage area and the total water outflow through the main stream of the tributary. The validity of the Hack's law for the plant leaf venation systems has been proved by the measurements of the authors. Some results are plotted in fig.5a and the corresponding schema is presented in fig.5b. As one can see the dependence $L_\Sigma = aS_\Sigma^\vartheta$ with $\vartheta = 0.5$ is obtained for all the studied 1030 images of the leaves. It is worthy to note the coefficient a in the linear dependence varies within surprisingly narrow physiological limits $a=1.71-2.32$, mining a wide diversity of the size, shape and evolutionary age of the studied leaves. While the statistical similarity of the plant leaf venations and the river systems is discussed in literature [19], the Hack's law, its appearance and validity for the liquid transport systems in the live nature have never been measured and discussed.

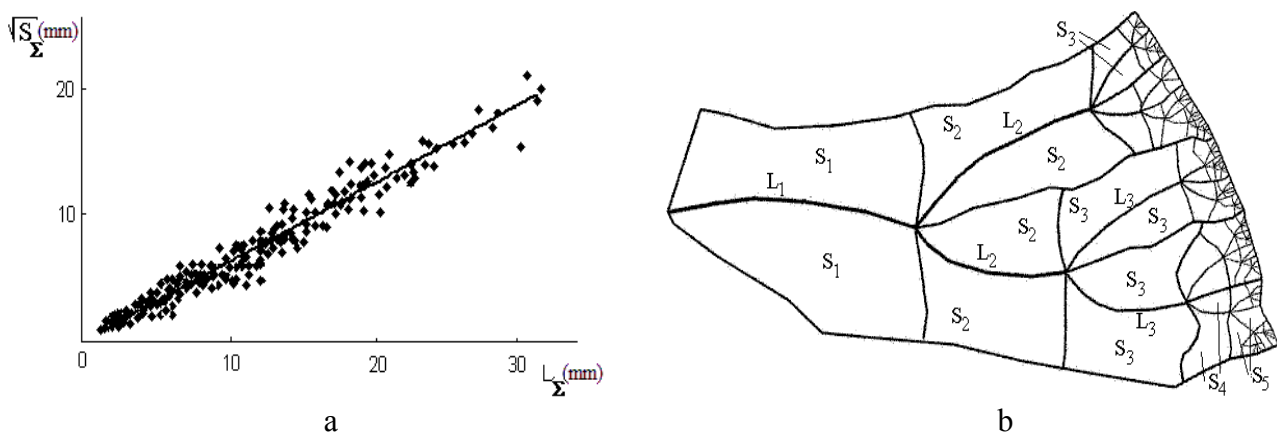


Figure 5 - An example of the linear dependence $\sqrt{S_\Sigma}(L_\Sigma)$ obtained for the measured digital images of the leaves (a) and the schematic of the distributions of S_Σ and L_Σ (*Cotinus Obovatus* leaf blade) (b)

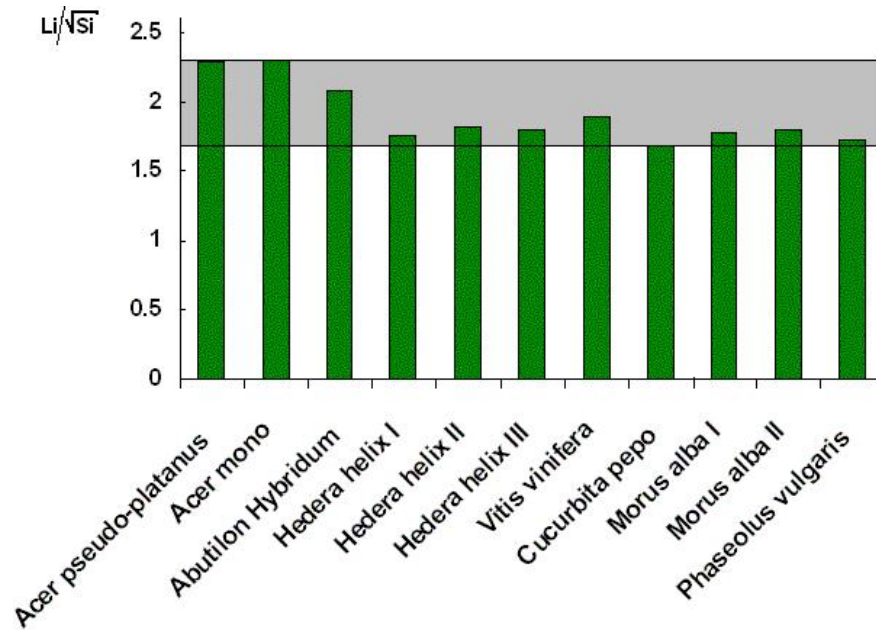


Figure 6 - Distribution of the coefficient in the linear dependence $L_{\Sigma}(\sqrt{S_{\Sigma}})$ obtained for different leaves

3. Mathematical models of the optimal liquid transport systems in the nature.

3.1. Murray's model of the optimal conducting element.

A theoretical explanation of the relationship (1) was proposed in [17,18] and based on the optimality principle for a single blood vessel, which had been treated as a rigid circular cylinder. The total energy W expended for the fluid flow, tube wall construction (construction costs) and nutrition and the energy consumption for the fluid nutrition (blood oxygenation and other metabolic costs) was proposed as an optimization criteria in the form

$$\dot{W} = Q^2 Z + \kappa V \rightarrow \min \quad (2)$$

where $Q^2 Z$ is the viscous dissipation, V is the volume of the tube (including the inner volume and the wall volume) and κ is a metabolic constant.

Solution of the problem (2) gives $Q^2 = \beta^2 d^3$, $\beta = \pi / 32 \sqrt{\kappa / \mu}$ for the optimal tube. From here for the flow through the bifurcation of the optimal tubes when $Q_0 = Q_1 + Q_2$, one can easily obtain the Murray's law

$$d_0^3 = d_1^3 + d_2^3 \quad (3)$$

which is sometimes called a Pythagorean Theorem in physiology.

Since the problem (11) has the same solution as the optimization problems

$$Q^2 Z \rightarrow \min \text{ at } V = \text{const}$$

and

$$V \rightarrow \min \text{ at } Q^2 Z = \text{const}$$

the optimal pipeline constructed basing on the Murray's law, possesses minimal hydraulic resistance at given volume or a minimal volume at given energy expenses, so existence of the sort of optimal conducting systems is intuitively clear.

The mechanism of formation of the optimal branching pipelines that correspond to the Murray's law is obvious, since for the Poiseuille flow the shear rate at the wall is $\tau_w = 32\mu Q / (\pi d^3)$, so in the optimal tube $\tau_w = \text{const}$. In that way when in a growing body the shear stress at the vessel wall is kept at a prescribed level $\tau_w = \text{const}$, the optimal tube (in the meaning of

the optimization criteria (2)) will be developed. The mechanism definitely exists in the blood vessels and is provided by mechanosensory cells in the wall endothelium (mechanoreceptors). The mechanoreceptors can estimate the shear stress at the wall and pass the corresponding signal into the middle (smooth muscle) layer. Depending on the signal the muscle contracts or relax, influencing the lumen area and keeping $\tau_w = \text{const.}$

For the plant leaf venations a model of an optimal pipeline with permeable walls has been proposed in [12]. Each vein on the leaf venation is considered as a rigid tube with porous walls. The pores are formed by the smaller branching of the next orders of branching and by the small pores which provided the liquid delivery to the surrounding plant cells directly. Both active and passive liquid transport governed by the hydrostatic and osmotic pressure drops between the conducting element and the surrounding media are taken into consideration. Solution of the optimization problem (2) was obtained. It was shown, for some model simplification (thin long conducting tubes) the Murray's law (1) with $\gamma \approx 3$ can also be obtained.

In that way it was shown that the similarity in construction of the long-distance fluid transport systems in plants and animals is provided by different mechanisms, which lead to the same relationship between the diameters of the vessels in the bifurcations.

3.2. The optimal relationship between the branching angles and the diameters of the vessels.

The model of the optimal branching has been proposed by Sir J.Lighthill [21]. The optimization criteria $Z_\Sigma \rightarrow \min$ has been used and the relationship $\cos \alpha = (d_1 / d_0)_4$ has been obtained. The same criteria has been used for the bifurcation of the rigid tubes and the corresponding relationships

$$\cos(\alpha_{\min, \max}) = \frac{(d_{\min}^3 + d_{\max}^3)^{4/3} \pm d_{\max}^4 \mp d_{\min}^4}{2d_{\max, \min}^2 (d_{\min}^3 + d_{\max}^3)^{2/3}} \quad (4)$$

or between the branching angles and the asymmetry coefficient

$$\alpha_1 = \arccos \left(\frac{(1 + \xi^3)^{4/3} + 1 - \xi^4}{2(1 + \xi^3)^{2/3}} \right), \quad \alpha_2 = \arccos \left(\frac{(1 + \xi^3)^{4/3} + \xi^4 - 1}{2\xi^2(1 + \xi^3)^{2/3}} \right), \quad \cos(\alpha) = \frac{(1 + \xi^3)^{4/3} - \xi^4 - 1}{2\xi^2} \quad (5)$$

have been obtained in [18]. The relationships (4)-(5) corresponds to the measured dependences.

3.3. Theoretical substantiation of the Hack's law in leaves.

A theoretical model of the viscous liquid flow in a microcirculatory cell of the leaf has been proposed in [13]. The microcirculatory cell of the plant leaf blade as a 2d area is restricted by a part of the leaf blade perimeter and the dividing lines separating the areas supplied by water and nutrients through different main veins. The optimization problem (2) has been generalized to the case of the bifurcation of the tubes with permeable walls in the form:

$$\dot{W} = \sum_{j=0}^2 (Q(8\mu L / (\pi R^4)))^2 + \kappa \pi R^2 L \rightarrow \min \quad (6)$$

where μ is the fluid viscosity. As it was shown by numerical calculations, the minimal total energy expense is reached when the relationships (4) or (5) between the diameters and branching angles are valid. Any small variation of the position (p,q) of the bifurcation point B (fig.7a) leads to significant variations of the branching angles within the experimentally observed limits $\delta\alpha \sim 10 - 25^\circ$ and insignificant changes in the value \dot{W} ($\pm 5 - 7\%$) in comparison with the optimal case (fig.7b). In that way the cost of a development mistake is relatively small and the mistake may be corrected at the consequent branchings by corresponding variations of their angles providing balance between the fluid outflow through the wall of the conducting system and its consumption by the cells in the corresponding influence domain.

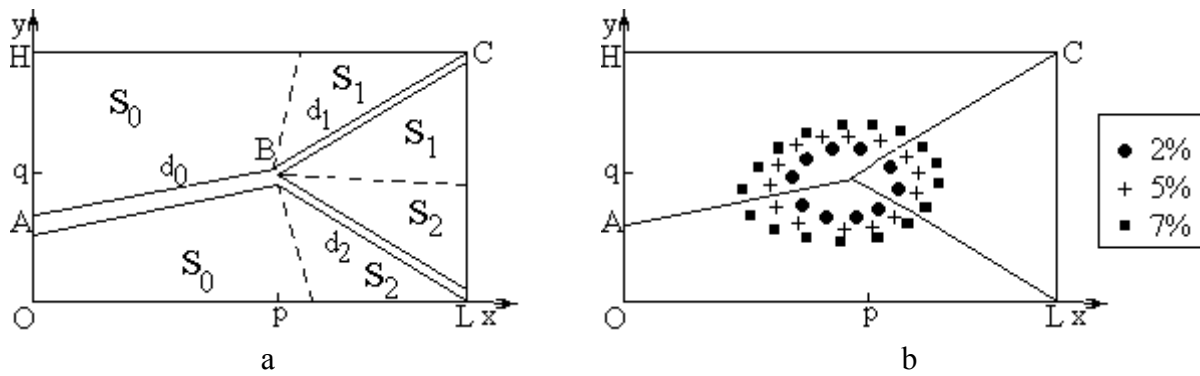


Figure 7 - Structure of the vein bifurcation inside a rectangular microcirculatory cell (a) and deviations of the total energy expenses of a small variation in the position of the junction B (b)

In contrast to the tubes with non-permeable walls (blood vessels) the total resistances $Z^{(1,2)}$ depend on the relation between the inflow Q_1 at the point of entry and the outflow Φ_1 through the permeable wall. In the event of $\Phi_1/Q_1 \ll 1$ or $\Phi_1/Q_1 = \text{const}$ in each tube of the branching system the total resistances of the bifurcation differ from $Z^{(0)} = Z_1^p + Z_2^p/2$ by the constant only. Thus the optimal bifurcation of the tubes with the permeable walls obeys the same Murray's law with $\gamma = 3$ as it is described in the section 2.1 and the similarity between the geometry of the mammalian and plant vasculatures take place.

Unlike the mammal vasculature the plant vessels are empty rigid tubes without live cell contents so they can not estimate either wall shear stress or any other mechanical parameters. Only the alive plant cells in the influence domains would do that. The possible mechanism of the optimal transport system formation can be connected with the balance between the sap amount that is needed for all the cells in the domain S and the corresponding flux Φ that can be provided by the lateral surface πDL of the conducting element. In that way it was shown that maintenance of the balance between the inflow of the liquid into the cell and its uniform absorption by the living cells in the growing plant leaf would lead to the optimal branching transport system formation and Hack's law validity. The mechanism can underlie the evolutionary optimization of the branching conducting systems in plants.

4. Efficiency of the liquid transport in the venations of different evolutionary ages and the constructal law.

Plant leaf venation experienced some substantial variations during the evolution. It is commonly accepted the following timeline: dichotomous - palmate - pinnate - parallel venation. The evolutionary diversity of the venation systems is not substantiated yet, so the constructal law may be suggested as a main constructive design principle of evolution of the leaf hydraulic structure. Basing on the theory of the steady viscous flow in a single rigid tube with permeable walls, the total hydraulic conductivity of the leaf venation can be calculated [12,13]. The main types of the leaf blade shape and venations can be considered as circles with embedded branching systems of tubes of given diameters and branching angles or a circle with a cut section of a given angle (fig.8).

The blade has been considered as filled with elements of the transportation system. The main vein or a set of main veins have been modeled by a rigid tubes with permeable walls. The angles between the veins have been taken from the measurement data. The second-order veins have also been introduced as tubes with permeable walls which lengths are determined by the edge of the blade. The branching angles ψ_j between the main and secondary veins have been given for each main vein and in the course of numerical calculations ψ_j vary from the measured values to $\pi/2$. The total hydraulic resistance Z of the transportation network has been calculated using the method developed in [6,12]. The dependences $Z(r, \theta)$ are presented in fig.9 for the model of the leaf blade

as a circle with 3, 5 and 7 main veins (fig.9a,b and c accordingly). The petiole is attached here at the perimeter of the blade.

The round blade with a petiole attached in its centre is regarded as the earliest evolutionary shape of the dicotyledonous leaves. Transition from the palmate to the pinnate and then to the parallel venations can be followed in the evolution and the parallel or camptodrome venation is regarded as an evolutionally optimal type.

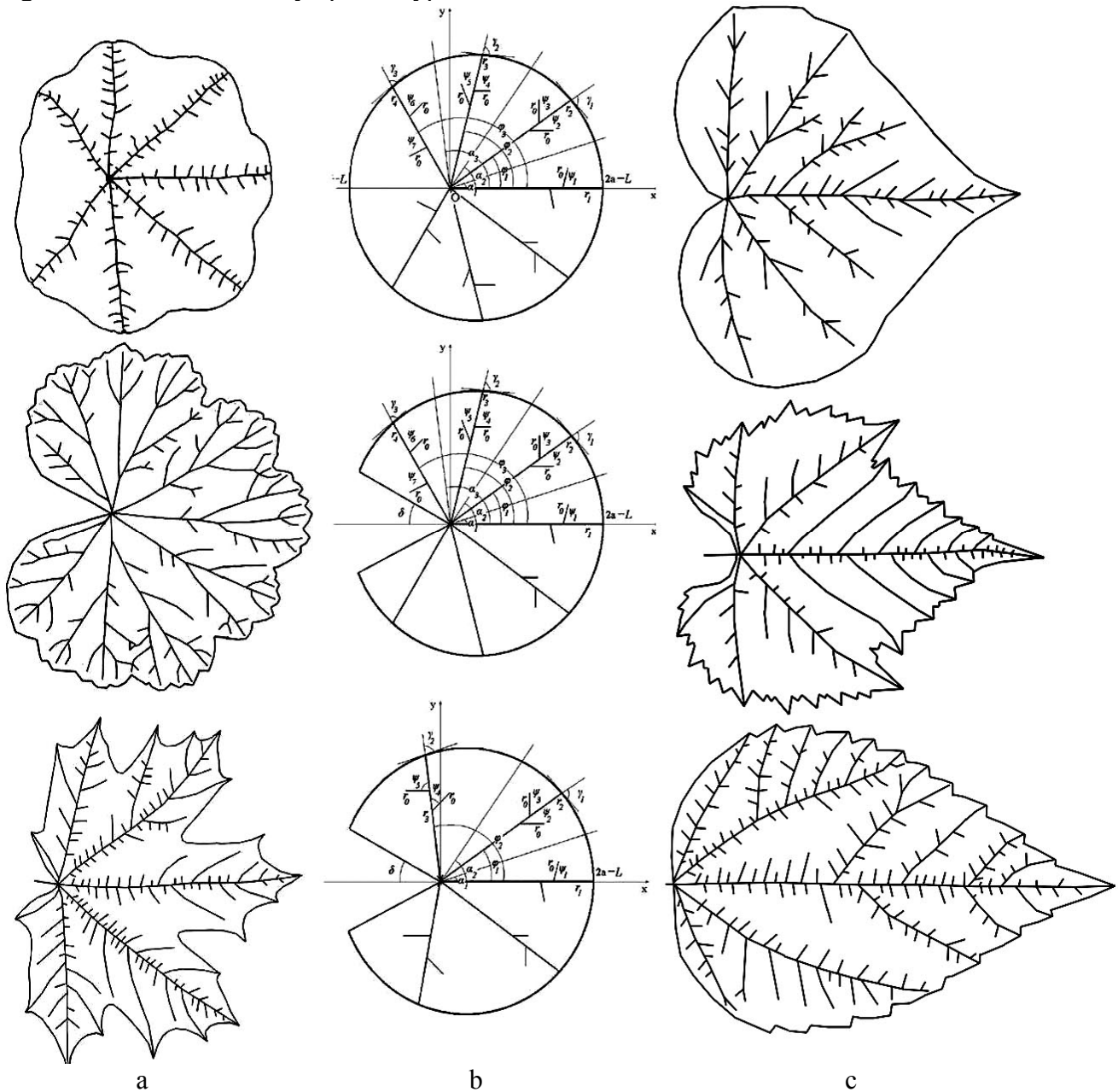


Figure 8 – Leaves of different venation types (palmate (a) and pinnate (c) conducting systems) and their mathematical models (b).

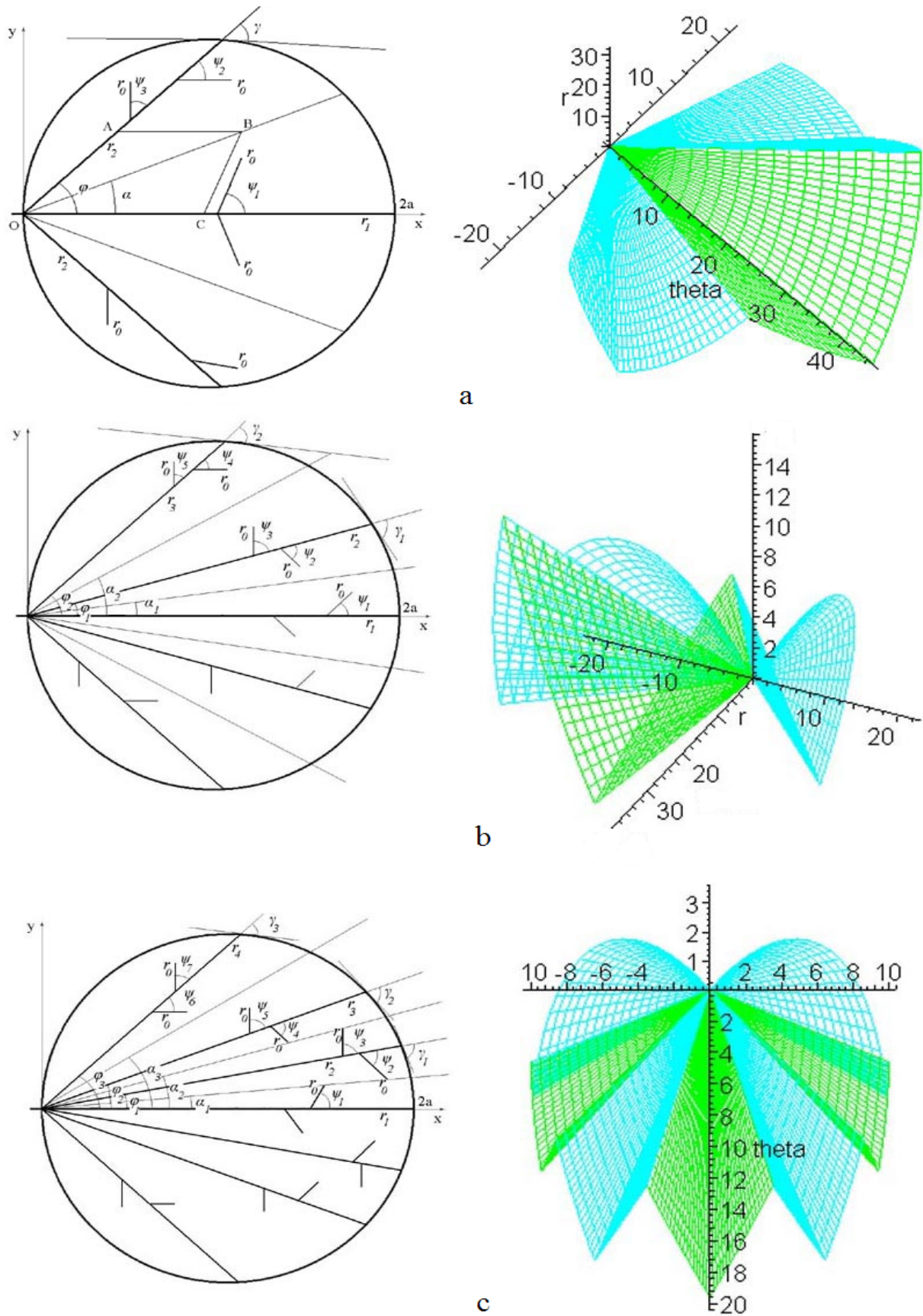


Figure 9 – construction of the conducting system and the hydraulic conductivity of a model of the leaf blade with 3 (a), 5 (b) and 7 (c) main veins (palmate venation).

The following regularities have been obtained as a result of the detailed computations:

- Any variation of the position of the petiole towards the perimeter of the blade leads to decreasing of the specific hydraulic resistivity $Z_h = Z / S$, where S is the area of the blade;
- In general, transition from the palmate to the pinnate venation leads to some decrease in Z , which depends on the number of the main veins in the model;
- Certain decrease in Z_h is always produced by cutting a segment near the petiole (fig.8b);
- Increasing of the branching angles ψ_j between the main and secondary veins leads to gradual decrease in Z and $Z \rightarrow \min$ when $\psi_j \rightarrow \pi/2$, which corresponds to the parallel venation.

In that way, all the variations in the position of the petiole, shape of the blade, type of the venation and branching angles observed in the plants at the evolutionary scale, provide gradual decreasing of the hydraulic conductivity of the liquid transportation system in the leaves, that is in perfect agreement with formulation of the constructal law given by A.Bejan: "For a finite-size system to persist in time (to live), it must evolve in such a way that it provides easier access to the imposed currents that flow through it."

5. Conclusions.

As it was shown by a comparative study of the data and own measurements on both arterial vasculations and plant leaf venations the relationships between the diameters d_j , branching angles φ_j , lengths L_j and the influence domains S_j are the same for the animal and plant organs and tissues and correspond to the model of the optimal pipeline that provide liquid delivery at the minimum total energy costs for the liquid motion and the pipeline construction and maintenance.

Control over the optimal pipeline formation in the developing plant leaf can be provided by maintenance of the balance between the liquid delivery and consumption, i.e. between the form and function. When the inflow of the water and nutrients is balanced by their consumption by the live cells of the leaf, the optimal tube with permeable wall is produced during the growth and development. When the vein is insufficient to supply the given drainage area the retardation of the cell divisions and growth in the drainage area due to the insufficient water delivery provides decreasing the area otherwise the new vein must be formed by a bifurcation of the main vein and increasing the total length of the pathway.

Some noticeable scatter of the measured data (fig.3b) can be explained by the relatively small energy costs of finite variations of the branching angles in a bifurcation (fig.7b).

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